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The ecological role of brachiopods in the Namuncurá MPA/Burdwood Bank, off southern South America

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Abstract

Extant brachiopods have been very little studied, despite being abundant along the Argentine marine platform and southern areas of the Subantarctic region. In this survey, we examined brachiopod assemblages from the Namuncurá MPA/Burdwood Bank area, off southern South America. The material ($n = 1203$) was recovered from 43 stations ranging in depth from 50 to 785 m during two oceanographic expeditions. Two species (*Liothyrella uva* and *Terebratella dorsata*) together represent 95% of the total abundance, with no significant decrease in body size over depths of 800 and 400 m respectively. A third species (*Magellania venosa*) was found in very small quantities shallower than 200 m, and with a large variation in size. There is a greater proportion (63.37%) of brachiopods with epibionts/encrusters, mainly bryozoans and tubiferous polychaetes, which are more common on the ventral valves of larger specimens, and mainly at depths shallower than 400 m. It was also observed that empty shells serve as a microhabitat for micromolluscs, mainly bivalves. The brachiopods showed signs of drilling predation (8.74%), but they were also prey for other unidentified predators. These predators left a different kind of damage concentrated around the shell margins (19.20%), which should be the subject of further investigation. Based on these results, it is interpreted that brachiopods from the Namuncurá MPA/Burdwood Bank appear to play an important role in the biotic and trophic interactions of benthic Subantarctic marine fauna, whether acting as substrates, refuges, or food.

Keywords SW Atlantic · Argentinean shelf · Subantarctic region · Biotic interactions

Introduction

Brachiopods are benthic marine invertebrates that dominated the Paleozoic seas (Bitner and Cohen 2013; Emig et al. 2013). Although they are not as numerous in the present as they were in the past (only 5% of known species are extant), they still develop in all seas and are often found in places with difficult access, such as crevices, caves, and other cryptic surfaces (Richardson 1997). For this reason, they have received more attention from paleontologists than biologists.

The Burdwood Bank is a submerged plateau that integrates the northern sector of the Scotia Ridge. It is located about 150 km east of Isla de los Estados (Staten Island) and about 200 km off the eastern extremity of the Argentine portion of Tierra del Fuego, in southern South America (Fig. 1). The area is especially relevant because of the great diversity of marine organisms, particularly benthic invertebrates, many of which are endemic to this area (Scottish National Antarctic Expedition 1908; Arntz and Brey 2003). Given its importance, in 2013, the Argentine government through the Pampa Azul program declared this region a marine protected area (MPA). From then on, it has been called Namuncurá, and it is the first open-sea (non-coastal) MPA in the country.

As a contribution to the Pampa Azul program, this paper focuses on the brachiopod assemblages recovered during two recent oceanographic expeditions to Namuncurá MPA/Burdwood Bank and the surrounding areas of southern

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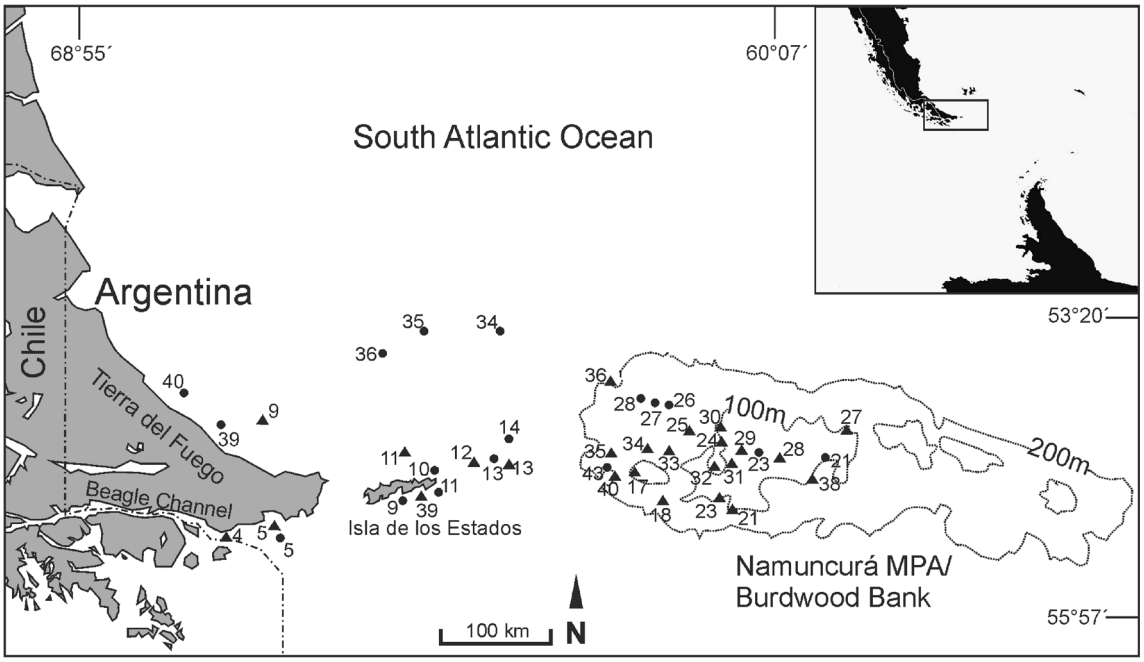

Fig. 1 Sampling sites of brachiopod assemblages collected during the two A.R.A. Puerto Deseado expeditions. Triangles correspond to the first year (2016) and circles to the second one (2017)

South America. In order to evaluate the spatial variations and ecological patterns of brachiopods in this area, we analyzed species composition, body size, and signs of biotic interactions on their shells between depths of 50 and 785 m.

Background

The first studies centered on living articulate brachiopods from southern South America which have shown that they are relatively well-distributed in areas shallower than 1000 m and that the settled specimens occupy a wide range of substrates, both hard and soft (McCammon 1970, 1973; Foster 1974, 1989; Roux and Bremec 1996).

Records of older brachiopods from Tertiary and Quaternary outcrops have also been documented in southern South America. Manceñido and Griffin (1988) analyzed the paleodistribution of *Bouchardia* from the uppermost Cretaceous–Paleocene to the Mio-Pliocene, which survives to the present in the sea around Brazil. Quaternary records along the Argentine Patagonian coast and in the Beagle Channel, at the southern tip of South America, were also mentioned by Feruglio (1950) and Gordillo (1990), respectively.

In this century, multiple studies have focused on modern brachiopods, including both dead and live specimens (e.g., Kowalewski et al. 2002; Carroll et al. 2003; Simões et al. 2004; Krause et al. 2010). These kinds of taphonomic studies centered on brachiopod assemblages provide information not only on the factors involved in the spatial distribution of brachiopods but also on ecological aspects, such as biotic interactions, and, even, on changes over time. For example, traces of incrusting and bioerosion on brachiopod shells provide information on the life position of the species, predators, and organisms living on (epibionts) or within the shells (endobionts) (Baumiller and Bitner 2004; Rodland et al. 2004; Rodrigues et al. 2008; Taddei Ruggiero and Raia 2010; among others). Besides, the analysis of these brachiopod assemblages has also made it possible to evaluate their temporal resolution (time-averaging) and the processes that cause the mixing of shells of different ages before their entry into the fossil record (Carroll et al. 2003; Krause et al. 2010). Despite these advances, in South America, these studies were carried out in the subtropical to tropical waters of the Brazilian platform (e.g., Simões et al. 2005a, 2007, 2009; Rodrigues and Simões 2010) and have not yet been made in the temperate to cold-temperate Argentine waters to the south. In this respect, it should be mentioned that the Brazilian fauna differs notably from the adjacent fauna living off the Argentine coast (see Simões et al. 2004).

Within this framework, a preliminary study in Namuncurá MPA/Burdwood Bank showed not only some affinities with other benthic communities in Argentine waters but also higher richness values compared to other productive areas on this shelf (Schejter et al. 2016). Cooper (1973) described six species of articulate brachiopods from Burdwood Bank. Three of them, *Liothyrella uva* (Broderip, 1833), *Terebratella dorsata* (Gmelin, 1791), and *Magellania venosa* (Dixon, 1789), were documented more recently on this bank by Schejter et al. (2016). These three species are widely distributed in southern South America (Foster 1974, 1989). Of the other three species

described by Cooper (1973), one of them, *Liothyrella oblonga*, is accepted as a synonym of *L. uva*, but the other two, *Aneboconcha obscura* and *Acrobrochus vema*, recognized as endemic to this bank, have not yet been collected again. It is important to mention that although both are valid species in the revised edition of the Treatise of Invertebrate Paleontology (Williams et al. 2006), their status requires a revision which integrates internal structure with molecular data. This situation is not surprising, given that the systematics/classification of brachiopods is based on internal skeletal structures since most of them are fossils, as mentioned previously.

In addition to this background and species composition, there are very few studies that address other aspects of brachiopods, particularly in the Argentine Patagonia and southern South America. One exception is a recent study by Morán et al. (2017) which focused on the role of brachiopods as a substrate for benthos. These authors analyzed the spatial variation of brachiopod epibionts in shallow waters (up to a depth of 100 m) between the latitudes of 40° and 55° S along the Argentine coast. They noted that higher latitudes had the highest overall rate of occurrence of encrusting organisms, mainly bryozoans. An even more recent study by Gordillo et al. (2018) analyzes the potential factors that regulate and limit the distribution of articulate brachiopods along the Argentine platform between 39° and 55° S. This work showed that the main factors that affect their distribution in this region were sediment grain size and water flow velocities and that larger sizes appear to be associated with areas rich in phytoplankton and suitable environmental water energy. However, more studies are still needed in southern South America, mainly below a depth of 200 m.

Material and methods

Study area

The Burdwood Bank is a platform with a total length of about 360 km in an E–W direction which narrows from 115 km in the west to 80 km in the east (Esteban et al. 2016). It is part of the North Scotia Ridge and corresponds to the eastward extension of the Fuegian Andes (Cavallotto et al. 2011). This seabed, composed of sand, gravel, and bioclasts, lies at a depth of 50–200 m with very low to null inclinations (Esteban et al. 2016). Its sides are formed of steep slopes that exceed 3000 m, and it has a total area of around 17,000 km^2, measured according to the 200 m isobaths.

During the last glacial maximum 24,000 years ago, sea level fell between 120 and 140 m below its current level, and the Burdwood Bank would have been a paleo-island of about 13,600 km^2 (Ponce and Rabassa 2012).

The main water mass in this region, commonly identified as Antarctic Intermediate Water (AAIW), is formed at the Antarctic Polar Front of the southeast Pacific, Drake Passage, the southwest Atlantic, and surrounding regions. From this zone, it is carried northward by the Malvinas Current along the South America Continental slope (Guerrero et al. 1999). At its origin, this current is a 400-m-thick layer with temperature ranging from 3.5 to 5 °C and an almost constant salinity of 34.2 PSU. It flows out of the Scotia Basin through two channels, west and east of the Burdwood Bank (Piola and Gordon 1989; Guerrero et al. 1999). Through the bank, the AAIW flows northwards in the upper 800 m. When comparing the western and eastern channels, important differences in the physical water properties can be observed. To the east of the Burdwood Bank (specifically east and north to Isla de los Estados), there is a strong contrast in the physical properties as a result of the mix of slope water and fresh water from the Beagle Channel and the Cape Horn continental shelf. However, to the west of the bank, the horizontal and vertical stratification is weak due to the homogeneity of the incoming AAIW and also because water formed in the area surrounding the Burdwood Bank is the same type (Guerrero et al. 1999). Given these oceanographic and bathymetric characteristics, the Burdwood Bank generates fronts and upwelling areas that lead to high concentrations of nutrients and high oxygen saturation (Piola and Gordon 1989; Peterson and Whitworth III 1989; Guerrero et al. 1999; Acha et al. 2004; Ulibarrena and Conzonno 2015).

Sampling

The material analyzed in this study was collected during two campaigns (March 2016 and May 2017) on board the ship RV A.R.A. Puerto Deseado in Namuncurá MPA/Burdwood Bank and the surrounding areas of the southern tip of South America, i.e., in the vicinity of the Tierra del Fuego mainland and Isla de los Estados (Fig. 1). Brachiopods, including articulated specimens and disarticulated valves, were collected from 43 stations at water depths of between 50 and 785 m (Table 1). Collection was mainly carried out using two trawls (Red Piloto and Red de Portones) and two dredges (Rauschert and Epibentónica Grande). The instruments used at each station for obtaining physical data include a SeaBird CTD (model SBE 19), a Seabird thermosalinograph (model SBE 21), and an echo-sounder SIMRAD EA600. Salinity and temperature data were acquired for each station (Table 1).

Data analysis

Subregions Stations located inside the Namuncurá MPA/Burdwood Bank are called here as "Burdwood," while the rest of the stations, outside the bank, are referred to as "outside the bank" or as "others."

Table 1 Sampling sites, physical factors registered at each station, and the total number (*n*) of articulate brachiopods recovered at each station. m, meters; °C, degree Celsius; PSU, practical salinity unit

Station	Year	Subregion	Depth (m)	Temperature (°C)	Salinity (PSU)	*n*
4	2016	Outside the bank	71	9.50	32.26	7
5	2016	Outside the bank	114	9.72	32.86	66
9	2016	Outside the bank	82	9.13	32.90	16
11	2016	Outside the bank	106	7.85	33.41	38
12	2016	Outside the bank	372	7.10	33.90	10
13	2016	Outside the bank	608	7.17	33.98	12
17	2016	Burdwood Bank	202	7.23	34.02	5
18	2016	Burdwood Bank	607	6.84	33.96	13
21	2016	Burdwood Bank	785	6.74	33.98	20
23	2016	Burdwood Bank	182	6.72	33.97	17
27	2016	Burdwood Bank	100	6.44	34.03	32
28	2016	Burdwood Bank	128	7.51	33.99	15
29	2016	Burdwood Bank	65	7.42	34.01	16
30	2016	Burdwood Bank	96	6.74	34.02	101
31	2016	Burdwood Bank	109	7.06	34.02	49
32	2016	Burdwood Bank	98	7.13	34.03	52
33	2016	Burdwood Bank	101	7.13	34.03	59
34	2016	Burdwood Bank	100	7.16	34.04	45
35	2016	Burdwood Bank	137	7.31	34.03	4
36	2016	Burdwood Bank	185	7.24	34.00	14
38	2016	Burdwood Bank	140	6.98	33.91	10
39	2016	Outside the bank	159	9.19	33.16	5
40	2016	Burdwood Bank	415	7.02	34.03	11
5	2017	Outside the bank	275	9.90	32.44	28
9	2017	Outside the bank	153	10.13	32.86	2
10	2017	Outside the bank	135	8.75	33.39	73
11	2017	Outside the bank	284	10.19	32.78	29
13	2017	Outside the bank	458	7.84	33.85	34
14	2017	Outside the bank	481	8.63	33.66	16
16	2017	Outside the bank	298	8.11	33.80	29
21	2017	Burdwood Bank	137	7.42	33.87	12
23	2017	Burdwood Bank	90	7.87	33.83	101
24	2017	Burdwood Bank	96	7.64	33.85	58
25	2017	Burdwood Bank	101	7.62	33.85	69
26	2017	Burdwood Bank	122	7.49	33.88	155
27	2017	Burdwood Bank	132	7.81	33.88	51
28	2017	Burdwood Bank	140	7.92	33.89	49
34	2017	Outside the bank	516	8.13	33.62	3
35	2017	Outside the bank	263	8.47	33.57	16
36	2017	Outside the bank	134	8.82	33.50	7
39	2017	Outside the bank	53	9.87	32.83	5
40	2017	Outside the bank	50	10.20	32.85	12
43	2017	Burdwood Bank	398	7.51	33.82	2
						1368

Brachiopod assemblages Brachiopod shells included articulated specimens and single dorsal and ventral valves. Articulated specimens are represented by live/dead individuals. The single valves were counted using the maximum number of individuals approach (given by the dorsal or ventral valves). Live specimens were relaxed in menthol for at least 2 h and later fixed in a 5% formaldehyde solution in seawater. According to some previous data, those species of

brachiopods with a flat dorsal valve and a convex ventral valve can experience the preferential transport of the convex ventral valve (Hallman et al. 1996). The proportions of dorsal and ventral valves were therefore calculated with a Chi-squared test in order to infer shell transport and residence time in the sediment water interface (Hallman et al. 1996; Simões et al. 2005b).

Species composition Species were identified following Cooper (1973) and Foster (1974), and the systematic position was updated according to the Treatise on Invertebrate Paleontology (Brachiopoda). The examined material was deposited in the CICTERRA collection, in Córdoba, Argentina.

Distribution and relationship between body size (length) and depth To explore bathymetric trends in body size, we plotted depth against length as a measurement of the body size of each specimen. This metric is highly correlated with body mass, together with linear measurements of the brachiopod shell (Foster 1974). Length was measured using vernier calipers to the nearest 0.1 mm. We tested the variation of body size with depth using least-square linear regression analysis in each species, obtaining the coefficient of determination (R^2) of each regression and their significance (p value).

Presence of encrusting/epibionts and predation traces To evaluate the role of brachiopods in the settlement of other invertebrates and algae, each articulated specimen was inspected for encrusting/epibionts. The presence/absence of each major taxonomic group (bryozoans, polychaetes, algae, etc.) was registered for each specimen. In the same way, empty articulated shells were also inspected to detect the presence of organisms that live inside. The proportion of specimens with encrusting/epibionts was computed for pooled data and also separately for data grouped by subregions (i.e., within the Burdwood Bank versus outside the bank) and depth. To estimate injuries caused by predation, we considered the presence of circular drill holes perpendicular to the shell surface, as well as other marks, such as breaks, which could have been produced by predators. In the case of drilling predation, the criteria used for the recognition of predatory drill holes follow previous works on this subject (see Kowalewski 2002 and references therein). Previously collected data on muricid predation on bivalves from southern South America (Gordillo and Archuby 2012, 2014) was also considered. Hence, in addition to drill-hole morphology, the presence in the region of potential predators, such as muricid and naticid gastropods, and traces of micro-rasping by the radula were also taken into account for a diagnosis. The incidence of predation of the three brachiopod species was calculated based on articulated specimens, and not considering single shells that are also part of the brachiopod assemblages. This was done to avoid taphonomic biases through asymmetry in the number of dorsal and ventral valves. Thus, the proportions of articulated drilled specimens of each species were pooled by depth, by subregions, and by the shell sector (ventral/dorsal or edge drilling). Finally, the articulated specimens with some kind of opening between the closed valves (not edge drilling), or the lack of part of a valve, suspected of being made by predators, were separated and counted. This analysis was carried out taking into account that the three species considered (*L. uva*, T. *dorsata*, and *M. venosa*) are able to repair the edge of their valves after attacks (Harper et al. 2009). However, instead of evaluating the predation failures, here, the suspected successful cases are considered, in order to compare them directly with the cases of predation by drilling. The proportion of specimens with injures suspected of being produced by predators were computed for pooled data and also separately for data grouped by subregions (i.e., within the Burdwood Bank versus outside the bank) and depth.

Results

Brachiopod assemblages and species composition

A total of 1203 brachiopod specimens (based on 1368 elements, including single dorsal and ventral shells) belonging to three species (*L. uva*, T. *dorsata*, and *M. venosa*; Fig. 2) were recovered (Tables 2 and 3). There were 870 articulated specimens, the majority alive at the time of collection. In general, empty shells presented external evidence of damage such as breakage or holes.

For the whole area sampled, the most common species was *L. uva* ($n = 688$; 49.65% in Burdwood and 76.25% outside the bank), followed by *T. dorsata* ($n = 454$; 45.94% in Burdwood and 17% outside the bank), and *M. venosa* in much lower proportions ($n = 61$; 4.41% in Burdwood and 6.75% outside the bank). These values indicate similar proportions of *L. uva* and *T. dorsata* within the bank, but much greater proportions of *L. uva* with respect to *T. dorsata* outside the bank. *M. venosa* was always in lower proportions.

If the depth range is taken into account, 33.83% of the brachiopods ($n = 407$) were recovered between 0 and 100 m depth, 49.88% ($n = 600$) between 100 and 200 m, and 16.29% from deeper waters (Table 3). *L. uva* was distributed throughout the range, *T. dorsata* was found up to 400 m, and *M. venosa* only occurred in the first 200 m (Fig. 3).

The proportions of dorsal and ventral valves of the three species varied significantly between the depths of 100 and 200 m ($p_{T.dorsata} > 0.001$; $p_{M.venosa} = 0.002$; $p_{L.uva} > 0.001$), while this proportion of *L. uva*'s valves varied between 200 and 400 m ($p_{L.uva} > 0.001$).

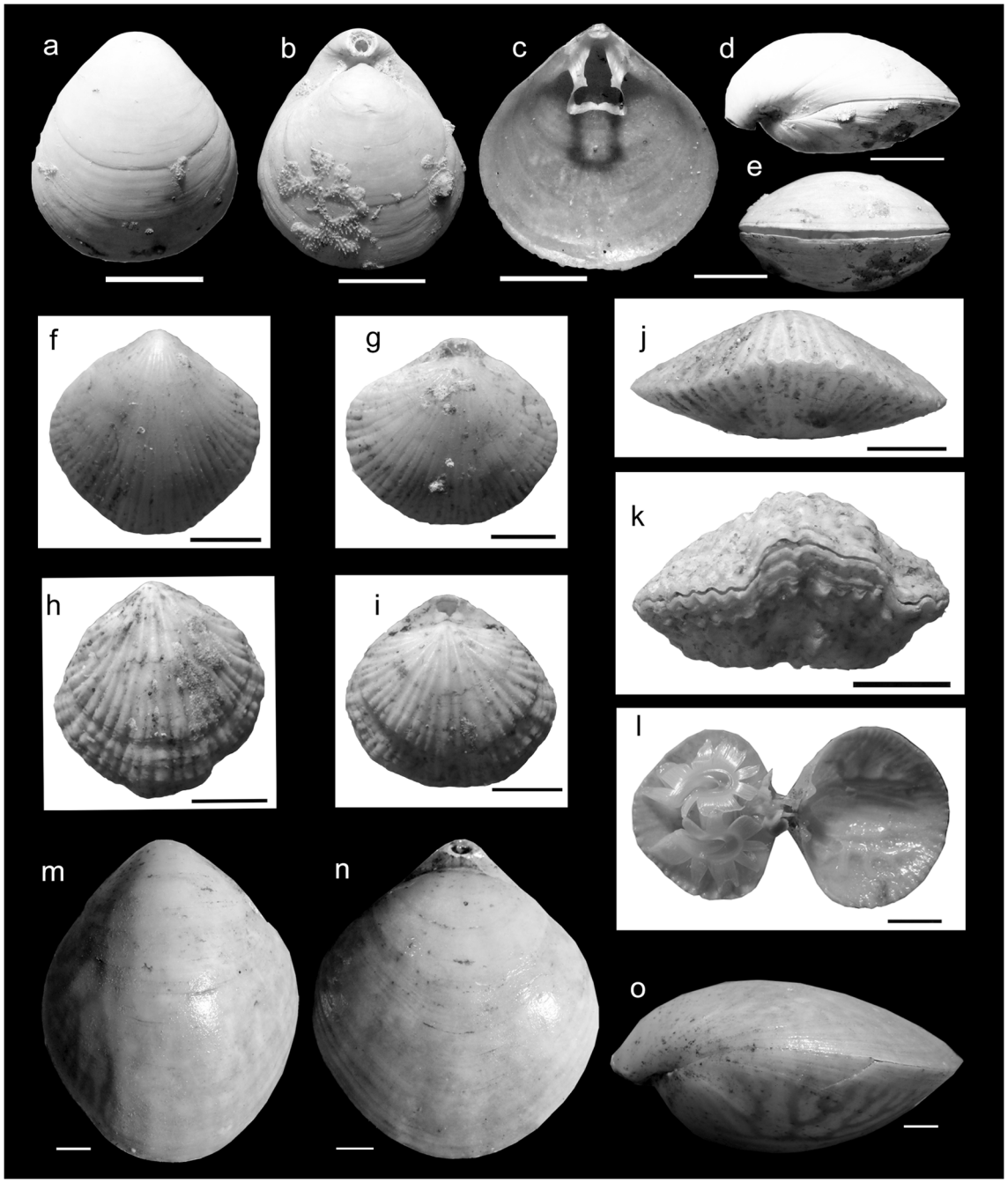

Fig. 2 Views of the three brachiopod species from Namuncurá MPA/ Burdwood Bank area; **a–e** *L. uva*; **a** ventral valve; **b** dorsal view with oval and labiate foramen; **c** interior view of dorsal valve; **d** lateral view; **e** anterior view; **f–l** *T. dorsata*; **f** and **h** ventral valve with conspicuous ribs; **g** and **i** dorsal view showing conspicuous ribs; **j** and **k** anterior views; **l** interior view; **m–o** *M. venosa*; **m** ventral valve with smooth surface; **n** dorsal view; **o** lateral view. Scale bar 1 cm

Table 2 Distribution of articulated (Art.) and single (dorsal, D; ventral, V) shells of the three species grouped by subregions

Number of stations	Subregion	Total	*n*	*L. uva*			*T. dorsata*			*M. venosa*		
				Art.	V	D	Art.	V	D	Art.	V	D
24	Burdwood	960	862	340	88	50	294	102	45	35	3	3
19	Others	408	341	152	108	53	36	22	14	13	10	0
		1368	1203	492	196	103	330	124	59	48	13	3

Table 3 Distribution of articulated (Art.) and single (dorsal, D; ventral, V) shells from the three species grouped by depth

Number of stations	Depth	Total	*n*	*L. uva*			*T. dorsata*			*M. venosa*		
				Art.	V	D	Art.	V	D	Art.	V	D
11	0–100	445	407	151	28	21	175	17	14	32	4	3
18	100–200	695	600	230	103	54	143	99	41	16	9	0
7	200–400	119	100	37	43	15	12	8	4	0	0	0
4	400–600	64	52	31	21	12	0	0	0	0	0	0
3	600–800	45	44	43	1	1	0	0	0	0	0	0
		1368	1203	492	196	103	330	124	59	48	13	3

Distribution and relationship between body size and depth

The distribution was plotted for the three species together in Fig. 4. The three brachiopod species showed no lineal association between body size (length) and their bathymetrical distribution (Fig. 5). *Liothyrella uva* ($R^2 = 0.06$; $p < 0.001$) was found over a range of 800 m. *Terebratella dorsata* ($R^2 = 0.08$; $p < 0.001$) was found only in the first 400 m and *M. venosa* ($R^2 = 0.32$; $p < 0.001$) appeared only in the first 150 m.

Presence of encrusting/epibionts

For the entire study area, there is a greater proportion of brachiopods with encrusters ($n = 545$; 63.37%) than without them, and this proportion is slightly higher within the protected area (i.e., 65.94% in the Burdwood Bank and 57.58% in neighboring regions). When discriminated by species, the highest percentages correspond to *T. dorsata* ($n = 268$; 80.72%) and, then, to *L. uva* ($n = 255$; 52.79%) and *M. venosa* ($n = 22$; 48.89).

Regarding the preference of encrusters for a particular size, in both *L. uva* (Fig. 6a) and *T. dorsata* (Fig. 6b), they are distributed throughout the size range, with less intensity in the smaller individuals (I and II size intervals) and greater intensity in the larger ones (III, IV, and V size intervals).

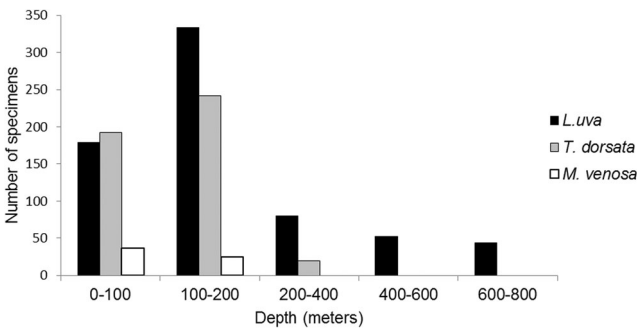

Fig. 3 Distribution of the three brachiopod species in depth intervals over a range of 800 m

In relation to the taxonomic groups, articulate brachiopods serve as a settlement for different groups, among which are bryozoans, calcareous polychaetes, including *Spirorbis* sp. and *Serpula* sp., Corallinaceae and other algae, juvenile brachiopods, and, sometimes, small gastropods and bivalves (e.g., *Kellia* sp., *Hiatella* sp., *Calyptraea* sp.). Of these groups, bryozoans are clearly dominant. No sponges were recognized in the samples analyzed. Encrusters on the internal surface of disarticulated valves (postmortem encrustation) show no differences between the taxonomic groups, except for the micromolluscs, mainly bivalves, which are preferably found inside empty articulated shells.

Finally, when analyzing the presence of specimens with encrusters according to depth (Table 4), it is observed that up to 400 m, there is a higher proportion of specimens with encrusters, while at greater depths, this proportion is inverted.

Figure 7 shows examples of valves with epibionts and encrusting.

Injuries from predation: drilling

Of the 43 stations considered, drilled shells were recovered from 25 (Table 5).

The incidence of predation based on 870 articulated specimens and 76 drilled articulated specimens gives a mean value of 8.74%. When the total number of specimens (articulated plus disarticulated) is considered, a slightly lower value of 7.07% is obtained (1203 specimens and 85 with drilling).

The predation values in the first 100 m, where all three species are present, are similar to each other and range from 5 to 6%. The highest predation values oscillate around 32% between depths of 200 and 600 m. This would explain why *L. uva* has a higher average value (10.98%) with respect to the other two species, which are not present in that depth range (Table 6).

When discerning the drilling depredation of *L. uva* in the two subregions, there is a noticeable difference between the Burdwood Bank and the peripheral region, which has higher values with respect to the bank. However, *T. dorsata* appears slightly more predated than *L. uva* within the Burdwood Bank

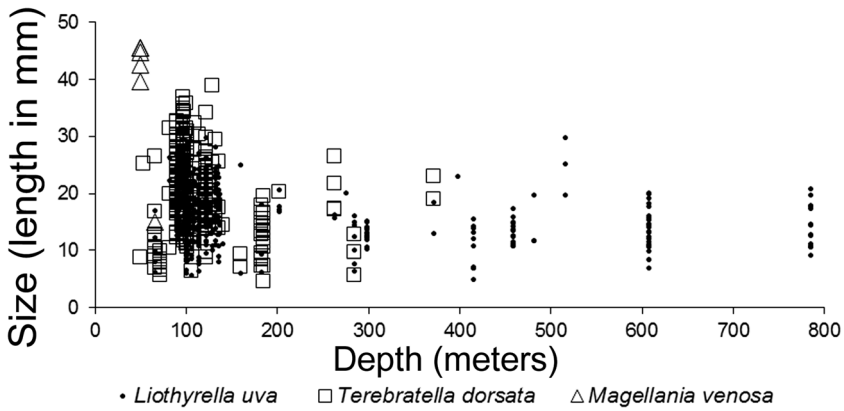

Fig. 4 Body size distribution of the brachiopods over a range of 800 m in the study region

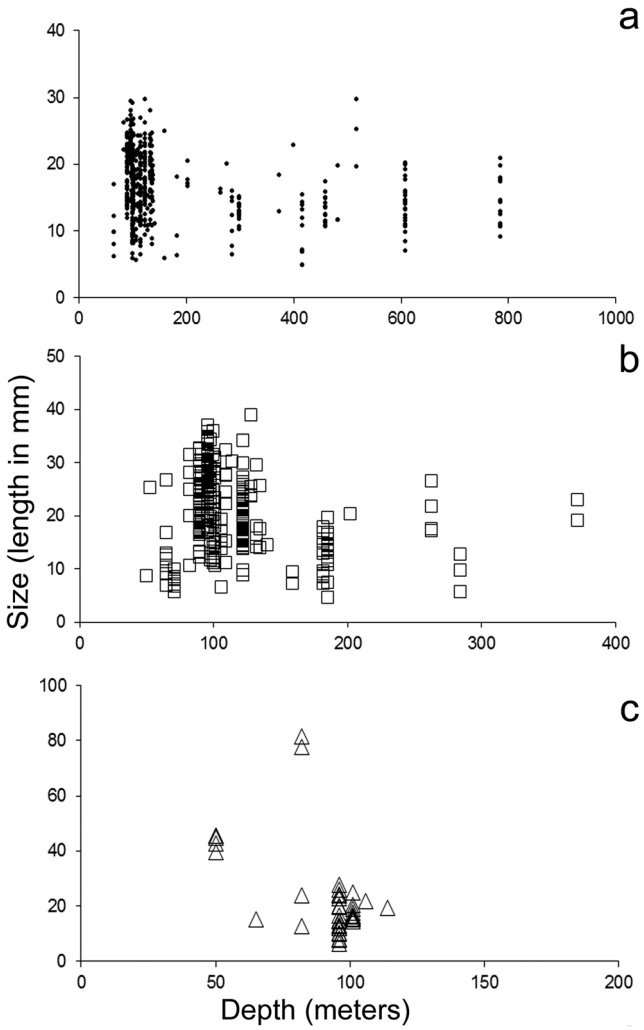

Fig. 5 Body size distribution of the three brachiopod species along the bathymetric profile in the study region. Simple linear regressions were not plotted due to their low goodness of fit. **a** *Liothyrella uva*, R^2 0.06, $p < 0.001$; **b** *Terebratella dorsata*, R^2 0.08, $p < 0.001$; **c** *Magellania venosa*, R^2 0.32, $p < 0.001$. Note different body size and depth scales on each diagram

but does not appear to be predated in the peripheral region (Table 7).

The highest percentage of holes in shells was found in ventral valves. There was a lower percentage in the dorsal valves and a small proportion in the marginal sector between the two valves. In this respect, it is important to mention that, in life, these organisms are more frequently found with the ventral (or pedicle) valve in the dorsal position. It is, therefore, interpreted that this preferential distribution could be linked to manipulation by the predator and better access to the upwards-facing ventral valve (Table 8).

Figure 7 shows examples of valves with drill holes.

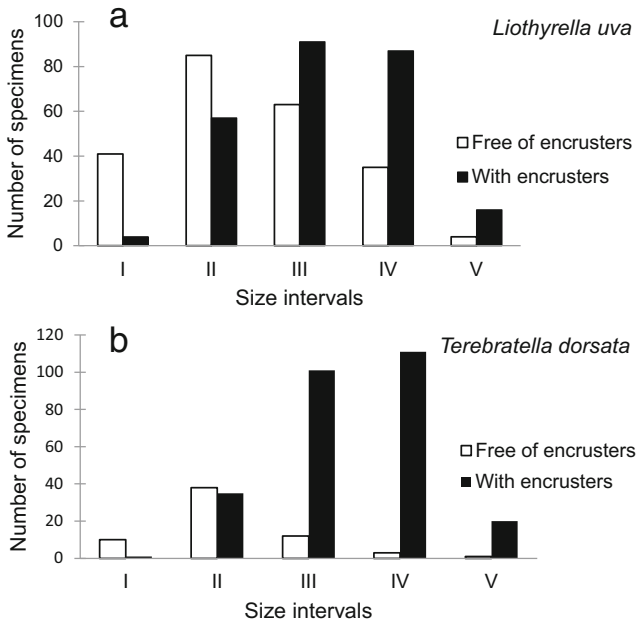

Fig. 6 Distribution of encrusters in *L. uva* (**a**) and *T. dorsata* (**b**) according to size ranges, from smaller (I) to larger (V). Size ranges in *L. uva*. I, 5–10 mm; II, 10–15 mm; III, 15–20 mm; IV, 20–25 mm; V, 25–30 mm. Size ranges in *T. dorsata*. I, 0–8 mm; II, 8–16 mm; III, 16–24 mm; IV, 24–32 mm; V, 32–40 mm

Table 4 Distribution of brachiopod specimens with and free of encrusters according to depth

Depth (m)	Free of encrusters	With encrusters	Proportion
0–100	100	278	>
100–200	140	232	>
200–400	16	25	>
400–600	28	3	<
600–800	31	7	<

Finally, when *L. uva* and *T. dorsata* drill holes were discriminated by size, there was no particular preference for a specific range (Fig. 8). In the case of *M. venosa*, only two valves presented a drill hole.

Other traces around the shell margins

We counted a total of 167 articulated specimens that had some kind of opening, breaks on the edges, or pieces missing from the valve. Based on the type of damage, the following was ascertained: 7.78% ($n = 13$) of the specimens have a notch on the edge; 54.49% ($n = 91$) have damage on the edge that affects only one of the valves (shown by a missing sector from minor to major, and irregular to sharp outlines); and 37.73% ($n = 63$) have damage on the edge, which includes the two valves and is shown by minor to major shell-breaking that looks like bite marks on the edge.

When accounting for these by subregion, it can be seen that 136 specimens (from 13 stations) with injures on the edges are from the Burdwood Bank, while only 31 (from 9 stations) are from outside the bank. When these marks are analyzed according to depth, similar proportions are observed up to 400 m, with a decrease, but no clear trend, with depth (Table 9).

Figure 7 shows examples of valves with injuries around the shell margins.

Discussion

This study is the first attempt to describe and characterize brachiopod assemblages from the open sea Namuncurá MPA/Burdwood Bank area, off southern South America. It is based on the analysis of 1203 brachiopod specimens (1368 elements, including single dorsal and ventral shells) recovered from 43 stations between depths of 50 and 758 m. Three brachiopod species (*L. uva*, *T. dorsata*, and *M. venosa*) were identified for the entire study area. Two of them (*L. uva* and *T. dorsata*) together represent 95% of the total abundance, and the third one (*M. venosa*) makes up the remaining percentage. Their presence is in agreement with previous studies in Patagonia and southern South America (McCammon 1970, 1973; Foster 1974, 1989; Roux and Bremec 1996; Gordillo et al. 2018). *Terebratella dorsata* and *M. venosa* also develop well in areas of high productivity, such as the Chilean fjords, where in some sites *M. venosa* was found growing on soft sediments, attached to grains of coarse sand (Foster 1989; Försterra et al. 2008).

When analyzing the composition of brachiopod assemblages discriminated by subregions, i.e., inside and outside the Burdwood Bank, it is observed that although the composition is the same, the proportion of the two main species differs. While similar proportions are found within the bank, *L. uva* is relatively more abundant than *T. dorsata* outside the bank. The similarity in species composition within an 800-m depth range could be because the study region, which includes the southern tip of South America, Isla de los Estados and Burdwood Bank, acts as an avenue of dispersal for brachiopods. This scenario was proposed by Foster (1989) to explain some of the connections between the fauna of South America and Antarctica, under which *L. uva* would have used the islands between South America and Antarctica as stepping stones.

When considering depth, there were no significant trends in size in any of the three species. However, *L. uva* and *T. dorsata* showed a slight tendency towards decreasing in size with depth, in the first 800 and 400 m, respectively. On the other hand, *M. venosa*, found in low numbers, shows considerable variation in size within a narrow depth range of 200 m. This slight tendency towards smaller size in deeper waters in the two dominant species is consistent with the study by Peck and Harper (2010) on terebratulid brachiopods, which also showed a trend of decreasing size with depth. However, in order to corroborate these trends, sampling would have to be intensified at depths greater than 800 m.

These brachiopod assemblages contain not only disarticulated valves but also a different proportion of valves, where ventral valves were always more abundant than the dorsal ones. This coincides with the fact that flat dorsal valves are more likely to be transported or are more fragile. This assemblage could therefore be interpreted as a local assemblage or an in situ brachiopod assemblage, where flat dorsal valves are in low proportions since they are prone to transport or disintegration.

Brachiopod assemblages as substrate and refuge for benthos

Regarding the presence of encrusting organisms on brachiopods, it is recognized that these assemblages, formed of living and dead specimens, constitute an important substrate for the settlement of different groups of benthos. Our results suggest that the ornamentation of *T. dorsata* with ribs is not an obstacle; on the contrary, it can be an advantage for the settlement

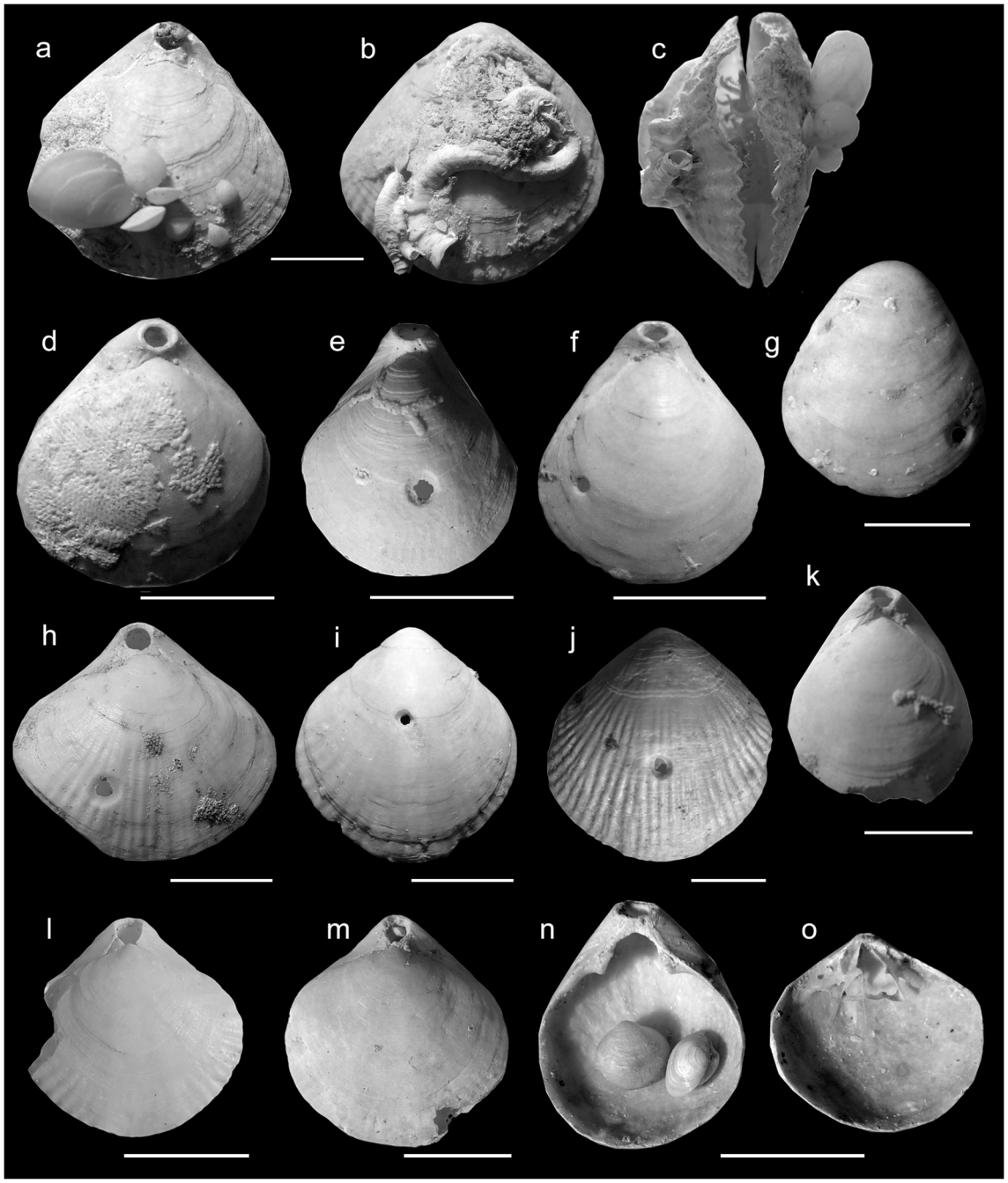

Fig. 7 **a**–**d** Encrusters/epibionts; **a**–**c** different views of one specimen of *T. dorsata* showing epibionts, mainly juvenile brachiopods on dorsal valve (**a**) and bryozoans and a tubiferous polychaete on the ventral valve (**b**); **d** specimen of *L. uva* with bryozoans on the dorsal valve. **e**–**j** Drillholes; **e**–**g**, drillholes on three different specimens of *L. uva*; **e** and **f** on dorsal valves and **g** on ventral valve; **h**–**j** drillholes on three different specimens of *T. dorsata*: **h** drillhole on a dorsal valve and **i** and **j** on ventral valves. **k**–**m** Injuries on the margins; **k** *L. uva*, dorsal view; **l** and **m** *T. dorsata*, dorsal views. **n**–**o** Nestlers; internal views of the ventral (**n**) and dorsal (**o**) valves of one specimen of *L. uva* showing two bivalves inside. Scale bar 1 cm

of epibionts, with respect to the other two species which have smooth surfaces.

Since encrusters are most commonly found attached to the ventral valve, this indicates that the individuals lived with the ventral valve in a dorsal position. In addition, the total absence of encrusters on the inferior (dorsal) valve of some specimens suggests that they could live more as semi-infauna than epifauna, with the lower valve buried or resting on the sediments. In the case of juveniles or small individuals without encrusters, this may be due to their small size, since there is less space available to colonize.

Table 5 Frequency of drillholes recovered from brachiopod assemblages at 25 stations

Year	Station	Depth (m)	*n*	*L. uva*	*T. dorsata*	*M. venosa*	Drilling	%
2016	5	114	65	56	4	5	11	16.92
	13	608	12	12	0	0	4	33.33
	18	607	13	13	0	0	1	7.69
	21	785	19	19	0	0	1	5.26
	23	182	17	4	13	0	3	17.65
	29	65	16	6	9	1	2	12.50
	31	109	46	19	27	0	1	2.17
	32	98	47	25	22	0	5	10.64
	33	101	58	32	13	13	3	5.17
	34	100	44	30	14	0	1	2.27
	38	140	8	6	2	0	1	12.50
	39	159	5	2	2	1	1	20.00
2017	10	135	56	52	4	0	6	10.71
	11	284	25	18	7	0	1	4.00
	13	458	27	27	0	0	9	33.33
	14	481	11	11	0	0	3	27.27
	16	298	23	23	0	0	11	47.83
	23	90	101	46	55	0	3	2.97
	24	96	58	28	30	0	4	6.90
	25	101	55	39	16	0	3	5.45
	26	122	135	57	78	0	7	5.19
	27	130	42	33	9	0	5	11.90
	34	516	3	3	0	0	1	33.33
	35	263	14	9	5	0	1	7.14
	40	50	9	1	1	7	1	11.11
			909	571	311	27	89	

Bryozoans appear to be the dominant encruster, followed by different calcareous polychaetes and algae, with juvenile brachiopods and patellid gastropods in minor proportions. Empty shells also serve as a microhabitat and as protection for different species of micromolluscs, both bivalves and gastropods. The lack of sponges is perhaps because they decay soon after death. Morán et al. (2017) found a predominance of bryozoans in southern Argentina at depths of up to 100 m. However, there is no other information from the region on the role of brachiopods as a substrate or protection for the different groups that make up the benthos. It is also unknown whether brachiopods also benefit from the camouflage these organisms could have provided. Given these results, and despite the very low diversity of brachiopods (only three species), the role of this group for settlement and protection of other benthic representatives is very important.

Table 6 Data of drilling predation of each species pooled by depth. Art. Articulated specimens

Depth (m)	*n*	*L. uva*			*T. dorsata*			*M. venosa*		
		Art.	Drilling	%	Art.	Drilling	%	Art.	Drilling	%
0–100	358	151	3	5.88	175	8	4.57	32	2	6.25
100–200	389	230	24	10.43	143	12	8.39	16	0	0
200–400	49	37	12	32.43	12	0	0	0	0	0
400–600	31	31	10	32.26	0	0	0	0	0	0
600–800	43	43	5	11.63	0	0	0	0	0	0
Total	870	492	54	10.98	330	20	6.06	48	2	4.17

Table 7 Data of drilling predation of each species pooled by subregion. Art. Articulated specimens

Subregion	*n*	*L. uva*			*T. dorsata*			*M. venosa*		
		Art.	Drilling	%	Art.	Drilling	%	Art.	Drilling	%
Burdwood	669	340	13	3.82	294	20	6.80	35	1	2.86
Others	201	152	41	26.97	36	0	0	13	1	7.69
	870	492	54	10.98	330	20	6.06	48	2	4.17

Drilling predation

Concerning the incidence of gastropod predation, the data obtained indicate that this type of predation occurs in the entire studied area but is higher outside the bank.

The analysis of drilling predation on the brachiopod *Bouchardia* from southern Brazil shows a low frequency of drilled shells (between 0.3 and 1.6%; Simões et al. 2007). Although this is lower than our results, they are comparable with the Burdwood Bank values. However, in the peripheral region of the bank, our results showed high drilling frequencies on brachiopod specimens of *L. uva*, with values up to 32%. Another example of extant brachiopods comes from the Mediterranean, in the study by Delance and Emig (2004) on *Gryphus vitreus*. These authors also found low values of drilling predation (lower than 1% in all stations), although in one station it reached up to 25.5%. Baumiller et al. (2006) mentioned a high mean value of 29.1% for specimens of *Basiliola beecheri* living in the Pacific. These authors also refer to the high variability of the incidence of predation on fossil brachiopods.

To assess patterns or trends of drilling predation in different regions, it would also be important to consider depth. Simões et al. (2007) obtained the low values mentioned in depths of less than 100 m, while Delance and Emig (2004) found a great variation between 100 and 300 m. In our work, we observed relatively low values in the first 100 m, a slight increase between 100 and 200 m, and a noticeable increase between 200 and 600 m. It could therefore be suggested that at least for this depth range the drilling frequency increases with depth.

When taken together with other published data, our results agree with the proposal by Baumiller et al. (2006) that brachiopod drilling frequencies are highly heterogeneous in space and time. For a better understanding of this kind of predation by durophagous predators, and for comparisons between different shelled potential prey, it would be interesting to incorporate molluscs, such as bivalves and gastropods, into future analyses.

With respect to the identity of predators, and taking into account the brachiopods' epifaunal mode of life, one could assume that they are killed by muricid gastropods (e.g., *Trophon* spp.) living in the region. This is reinforced by experimental work by Harper and Peck (2003), who demonstrated that the muricid gastropods *Trophon longstaffi* could produce drill holes on *L. uva*; while these drill holes are generally circular, they can vary in shape. However, given the plasticity of the brachiopods, adopting a semi-infaunal mode of life within fine sediments, this leads us to consider the possibility that naticids could also be potential predators.

Table 8 Data of drilling predation of each species pooled by the sector of the valve with holes

Position	*L. uva*	*T. dorsata*	*M. venosa*	%
Dorsal	19	4	1	31.58
Ventral	34	13	1	63.16
Edge	1	3	0	5.26
	54	20	2	

Other injuries and potential predators

Finally, when considering other shell damage attributable to predators, a higher incidence than for the previous case was

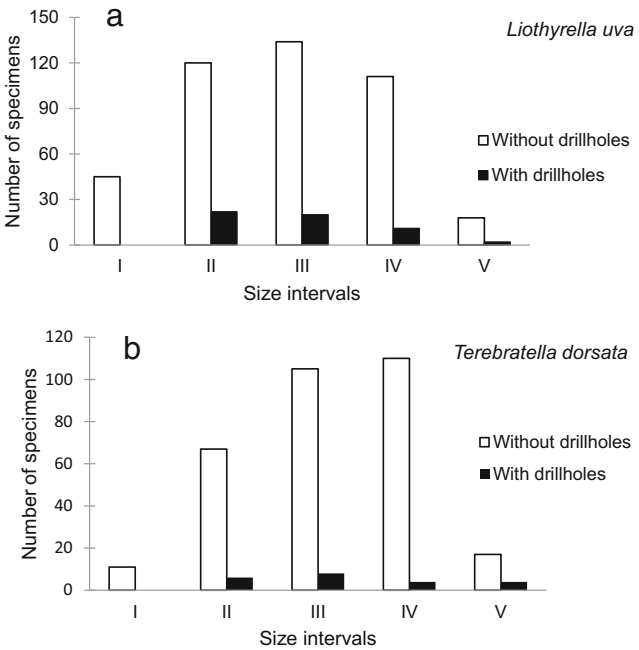

Fig. 8 Distribution of drillholes in *L. uva* (**a**) and *T. dorsata* (**b**) according to size ranges. See intervals for each species in Fig. 6

Table 9 Distribution of brachiopod specimens with damage on the margins according to depth

Depth (m)	*n*	Damage	%
0–100	358	78	21.78
100–200	389	73	18.77
200–400	49	10	20.41
400–600	31	0	0
600–800	43	6	13.95
	870	167	19.20

obtained. Unfortunately, there is little accurate information in literature on these kinds of brachiopod marks on living species (see Harper 2011). For the study region, potential predators could involve fish, octopuses, and crustaceans, according to the main groups of predators present in the region, and based on unpublished data from the two campaigns. For now, we do not know the identity of the predators, but there are basically two patterns: the first affects both valves, and could have been produced by certain fish (e.g., *Patagonotothen*) while grazing on polychaete tubes living on brachiopods as epibionts, and may not have been intentional. The second affects the margin of a single valve and leaves irregular or sharp outlines; this pattern is more difficult to elucidate, but it could have been caused by the beak of an octopus or the claw of a decapod. In any case, there is still a lot to investigate in this field.

When comparing the drilling incidence with supposed shell-breaking by predators, our results would indicate that inside the Burdwood Bank crushing predators that break shells are more important than drillers. On the other hand, outside the bank, these proportions are inverted, which highlights the need for more tools to analyze the trophic web in both regions. The specimens examined in this study thus indicate that brachiopods from the studied region were not only subjects of drilling predation but were also the prey of other unidentified predators which cause different kinds of damage to the shells. It is important to mention here that these signs of direct biological interactions are robust indicators of predator–prey interactions in the past and present (Vermeij 1987; Kowalewski and Kelley 2002; Kelley et al. 2003); so, we will continue working on this issue.

Endobionts: only in the dead or also in the living?

A final aspect that should also be deepened in future studies is to evaluate the interaction between brachiopods and the molluscs living inside their shells. In this work, we found small bivalves inhabiting as nestlers inside shells, particularly in specimens that presented the injuries described previously. However, the possibility remains that micromolluscs can also nest in the internal cavity of living brachiopods, giving rise to interactions of commensalism, mutualism, or even parasitism. In this respect, there are examples of crustaceans and polychaetes that live inside extant brachiopods (Feldmann et al. 1996; Rodrigues et al. 2008).

Conclusions

Brachiopods from the Namuncurá MPA/Burdwood Bank region appear to play an important role in the biotic and trophic interactions of benthic marine fauna, whether acting as substrates, refuge, or food.

As there is so little available information, it is important to intensify these studies. This will also provide input for other investigations focused on the role of biotic interactions in shaping ecological communities; it will also help to evaluate the ecological conditions that establish large-scale evolutionary trends. Further studies centered on modern brachiopod assemblages will provide useful, significant, and more accurate information for further paleontological interpretations of fossil brachiopod assemblages.

Additionally, and as part of a marine biodiversity conservation program, genetic studies on brachiopods from the Namuncurá MPA/Burdwood Bank are required. These would complement the diagnoses made from the shells and could lead to a greater understanding of the connection between South American and Antarctic brachiopods.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities mentioned in the acknowledgements.

Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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